

LIFE HISTORY OF *TRUPANEA CALIFORNICA* MALLOCH
(DIPTERA: TEPHTRITIDAE) ON *GNAPHALIUM* SPP. IN
SOUTHERN CALIFORNIA

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Abstract. — *Trupanea californica* Malloch is a multivoltine, nondiapausing, oligophagous tephritid reproducing in the flower heads of *Gnaphalium* and *Anaphalis* spp. in the tribe Inuleae of the Asteraceae in southern California. The larvae feed mainly on the ovules and achenes, and only incidentally on the receptacle. Unlike other flower head-infesting, nongallicolous Tephritidae, the puparia commonly are oriented with their long axes angled at 45° or less, or even parallel, to the receptacle surface. The egg, second and third instar larvae, and puparium are described and figured. The most noteworthy feature of the immature stages are the open, apparently functional lateral spiracles on the second and third thoracic segments and all abdominal segments except the last of the third instar. The presence of these spiracles seemingly contradicts the amphineustic tracheation ascribed to larvae of all Muscomorpha, including the Tephritidae.

Key Words: Insecta, *Trupanea californica*, spiracles, larval tracheation, immature stages, *Gnaphalium*, *Anaphalis*

Despite its namesake, *Trupanea californica* Malloch (Diptera: Tephritidae), heretofore was not very well known in California or elsewhere. Our study of this tephritid continued a series of life histories of different species of *Trupanea*, the largest and most commonly encountered genus of nonfrugivorous fruit flies in California (Foote and Blanc 1963, Cavender and Goeden 1982, Goeden 1987a, 1989)

MATERIALS AND METHODS

This paper was based on rearing records, photographs, and laboratory notes of dissections of selected samples of mature flower heads of Asteraceae infested by *T. californica* from among the many samples collected annually throughout California in the manner described by Goeden (1985). Field observations of adult behavior were made on *Gnaphalium beneolens* Davidson

at Hemet Lake, San Bernardino National Forest (southern section), Riverside Co., during August and September, 1988 and 1989. Adults studied were either swept from *G. beneolens* at Hemet Lake or reared in glass-topped sleeve cages in the insectary of the Department of Entomology from bulk flower-head samples of this and other species of *Gnaphalium* collected elsewhere in California (Goeden 1985). Behaviors of adults were observed in screen-topped, clear plastic laboratory cages or in 9-cm dia., disposable, clear-plastic Petri dishes provisioned with honey and water (Goeden and Headrick 1990, Headrick and Goeden 1990c). Flies were reared from puparia dissected from flower heads and held separately in cotton-stoppered, glass, shell vials within humidity chambers at 22–24°C and 76% R.H.

Plant names used in this paper follow

Munz (1974). With one exception, the materials, methods, format, and nomenclature used to describe the immature stages follow Headrick and Goeden (1990a) and Goeden and Headrick (1990); i.e. glacial acetic acid (100%) was added to the rehydration and dehydration steps to maintain natural size and shape of larvae. Means \pm SE are used throughout this paper. Voucher specimens of reared adults of *T. californica* reside in the research collection of RDG; preserved specimens of eggs, larvae, and puparia are in the research collection of immature Tephritidae of DHH; vouchers of plants were stored in the Herbarium of the University of California, Riverside, only if pressed specimens were scarce or from northern California.

RESULTS AND DISCUSSION

Taxonomy

Malloch (1942) described *T. californica* as a *Trypanea*, and in part as *Trypanea microsetulosa* Malloch, which Foote (1960) synonymized with *californica* in his revision of the genus in North America north of Mexico. Foote (1960) and Foote and Blanc (1963) provided photographs of right wings of females, but adults otherwise have not been illustrated. The immature stages heretofore have neither been illustrated nor described.

Egg.—The egg (Fig. 1A) is smooth, shiny, elongate-ellipsoidal, white, and rounded at the end opposite the reduced, buttonlike, 0.02-mm pedicel. Twelve eggs averaged 0.49 ± 0.006 (range, 0.46–0.52) mm in length and 0.17 ± 0.003 (range, 0.16–0.18) mm in width. Thus, eggs of *T. californica* are similar in appearance to, but slightly shorter and thinner on average than, eggs of *T. bisetosa* (Coquillett) (Cavender and Goeden 1982), *T. conjuncta* (Adams) (Goeden 1987a), and *T. imperfecta* (Coquillett) (Goeden 1988).

Third instar larva.—Fully grown larvae ($n = 6$) of *Trupanea californica* are white, barrel shaped, tapered anteriorly, rounded

posteriorly and measure ca. 3 mm in length (Fig. 2A). The gnathocephalon is conical and bears rugose pads on its anterior face (Fig. 2B-1). The mouth hooks are tridentate, and the median oral lobe is laterally flattened and tapers to a point anteriorly (Fig. 2C); however, unlike *Paracantha gentilis* Hering (Headrick and Goeden 1990a), the ventral lobe bears no papillae. The gnathocephalon surrounds the mouth lumen and has comparatively small petals dorsad of the mouth hooks (Fig. 2D-1) (cf., Headrick and Goeden 1990a, Goeden and Headrick 1990). The dorsal sensory organs each consist of a single dome-shaped papilla (Fig. 2D-2) and lie dorsad of the anterior sensory lobes (Fig. 2D-3). The lateral sensory lobes bear two sensilla, a finger-like projection, and an open pore (Fig. 2D-4). The posterior portion of the gnathocephalon is smooth (Fig. 2B).

The anterior portion of each segment posterior to the gnathocephalon is circumscribed by rows of minute acanthae (Fig. 2B-2). The prothorax bears rugose pads as well as rows of acanthae on its anterior portion (Fig. 2B), which is unusual among nonfrugivorous larvae described thus far (cf., Headrick and Goeden 1990a, Goeden and Headrick 1990). However, this is a consistent feature of *Trupanea* larvae examined to date (Headrick, unpublished data). The anterior thoracic spiracles are located dorsolaterally on the posterior portion of the segment, and each spiracle is topped with four tubular openings (Fig. 2E). The prothorax also bears several stelex sensilla, but none of the typical domed sensilla (cf., Foote 1967, Headrick and Goeden 1990a).

Each segment of the body posterior to the prothorax, excluding the caudal segment, has a lateral spiracular complex consisting of a lateral sensillum (Fig. 2F-1) and a vestigial lateral spiracle (Fig. 2F-2). The sensillum is dome-shaped with a central pore which is typical of nonfrugivorous larvae described thus far (Fig. 2F-1). Among larvae of other nonfrugivorous species, the number of such sensilla varies from one to four per segment (Goeden and Headrick 1990). Anterior to

this sensillum on each body segment is an open, lateral spiracle (Fig. 2F-2, 2G), which in *Stenopa affinis* Quisenberry and other tephritid species examined to date usually appears as a closed ecdysial scar, like that on the posterior spiracular plate (Goeden and Headrick 1990, Headrick, unpublished data, Fig. 2H-3) (the lateral spiracular scar was incorrectly identified as a depressed sensillum in Goeden and Headrick 1990). However, in *T. californica*, these open lateral spiracles are presumably functional, as each opens into a lateral commissure of the tracheal system (Fig. 2G). The lateral commissures are always present in tephritid larvae and may be seen on the inside walls of an empty puparium (Snodgrass 1924, Headrick and Goeden 1990a, Headrick, unpublished data). These open lateral spiracles in *T. californica* are an important discovery because the larvae of all Muscomorpha, including the Tephritidae, are considered amphipneustic! Indeed, amphipneustic tracheation is apomorphic with respect to the ground plan of the order Diptera and plesiomorphic to the Muscomorpha; i.e. such a character should help to define the primitive sister group of the Muscomorpha (McAlpine 1989). However, the discovery of open lateral spiracles suggests that a more primitive holopneustic condition may be restored (sensu Snodgrass 1924) in tephritids. This finding provides further evidence that larval Diptera characters used today to define relationships are in need of more detailed examination. As recently noted by Headrick and Goeden (1990a), the discovery of anatomically complex structures in tephritid larvae, such as the median oral lobe, and in the present study, the open lateral spiracles, highlights the need for further morphological research on characters that may be useful phylogenetically.

The frugivorous larvae of *Rhagoletis pomonella* Walsh examined by Snodgrass (1924) had lateral commissures on the mesothorax and all but the last abdominal segments inside the puparium. Snodgrass (1924) also noted that the lateral spiracles

were impossible to see by surface examination until the "skin hardens to form the puparium." Today, with the SEM, these lateral spiracles are visible on at least the third instar of tephritid larvae, as are the associated sensilla which Snodgrass (1924) was unable to observe.

The posterior segment is rounded and bears the posterior spiracular plates (Fig. 2H). Each plate bears three elongate-oval rimae (Fig. 2H-1, the longest rima was 0.04 mm long), four interspiracular processes with six to eight branches each (the longest process was 0.01 mm, Fig. 2H-2), and an ecdysial scar (Fig. 2H-3).

Second instar larva.—A single second instar larva was greyish white, sub-spheroidal, and measured 0.35 mm. The gnathocephalon had fewer rugose pads on the anterior face than the third instar (Fig. 3A-1). The mouth hooks are bidentate. The median oral lobe is narrowly tapered anteriorly like the third instar. The dorsal sensory organs are single domed papillae (Fig. 3A-2). The anterior sensory lobes bear terminal, lateral and pit sensory organs (Fig. 3B-1, -2, -3), and the lateral sensory lobes bear two sensilla as described for the third instar (Fig. 3C).

The segments posterior to the gnathocephalon are circumscribed by two or three rows of acanthae, unlike the third instar, which has more than 10 irregular rows of acanthae per segment. The posterior spiracular plates bear three elongate-oval rimae (Fig. 3D-1, the longest rima was 0.0015 mm long) and four interspiracular processes composed of two to four branches each (the longest process was 0.001 mm long, Fig. 3D-2).

Second-instar larvae having fewer interspiracular branch numbers, fewer rugose pads, and bidentate mouth hooks also were reported for second instars of *P. gentilis* (Headrick and Goeden 1990a).

Puparium.—The puparium is elongate-oval, barrel shaped, rounded on the ends, and black (Fig. 1C, 4A). Thirty-four puparia measured 1.9 ± 0.05 (range, 0.9–2.4) mm

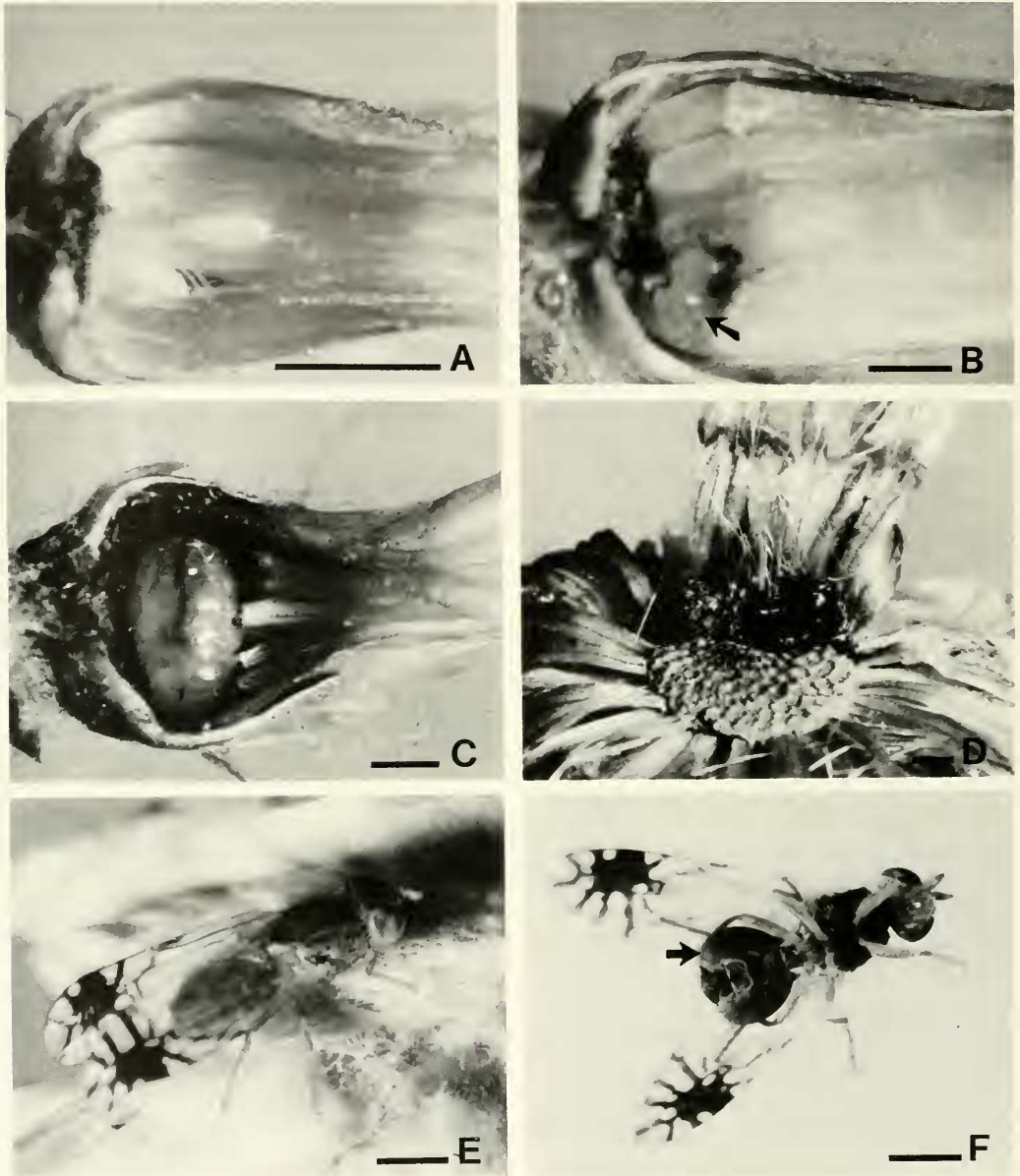
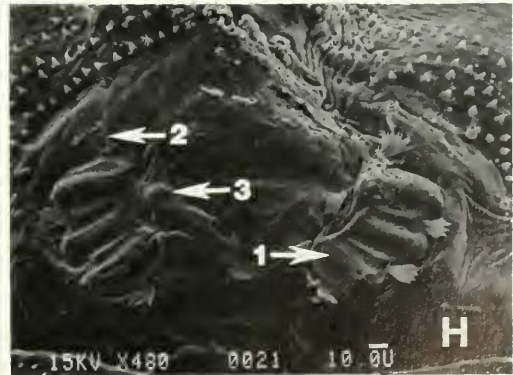
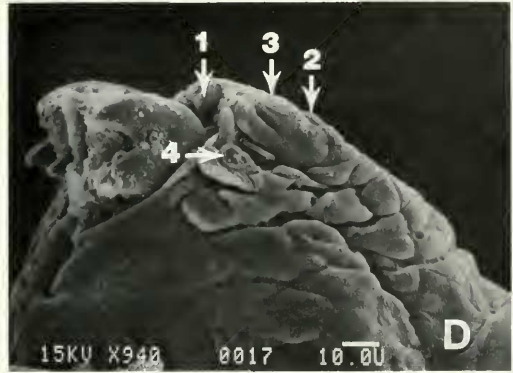
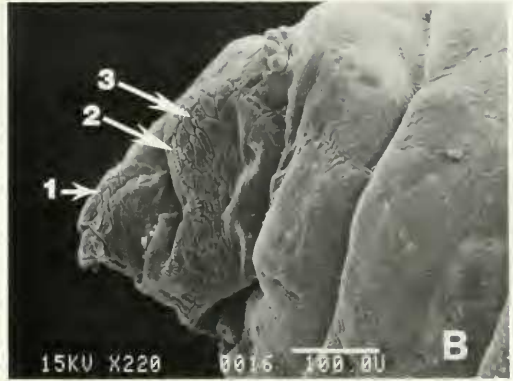


Fig. 1. Life stages of *Trupanea californica*. A. Two pairs of eggs in young flower head of *Gnaphalium beneolens* in laboratory, one pair per head is normal; B. Early instar larva (arrow) feeding on ovules in head of *G. beneolens*; C. Third instar larva feeding in achene layer in head of *G. beneolens*; D. Puparium on periphery of receptacle of head of *G. californicum*; E. Adult male in typical resting position on head of *G. beneolens*; F. Male with inflated abdominal pleura (arrow). Lines = 1 mm.

Fig. 2. Third-instar larva of *T. californica*. A. Habitus. B. Anterior end, lateral view; 1, rugose pads; 2, acanthae; 3, rugose pads. C. Anterior end, ventral view; 1, median oral lobe. D. Anterior end, lateral view; 1, petals; 2, dorsal sensory organs; 3, anterior sensory lobes; 4, lateral sensory lobe. E. Anterior thoracic spiracle. F. Lateral spiracular complex; 1, sensillum; 2, spiracle. G. Detail of the open lateral spiracle. H. Caudal segment, posterior view; 1, rima; 2, interspiracular process; 3, median ecdysial scar.



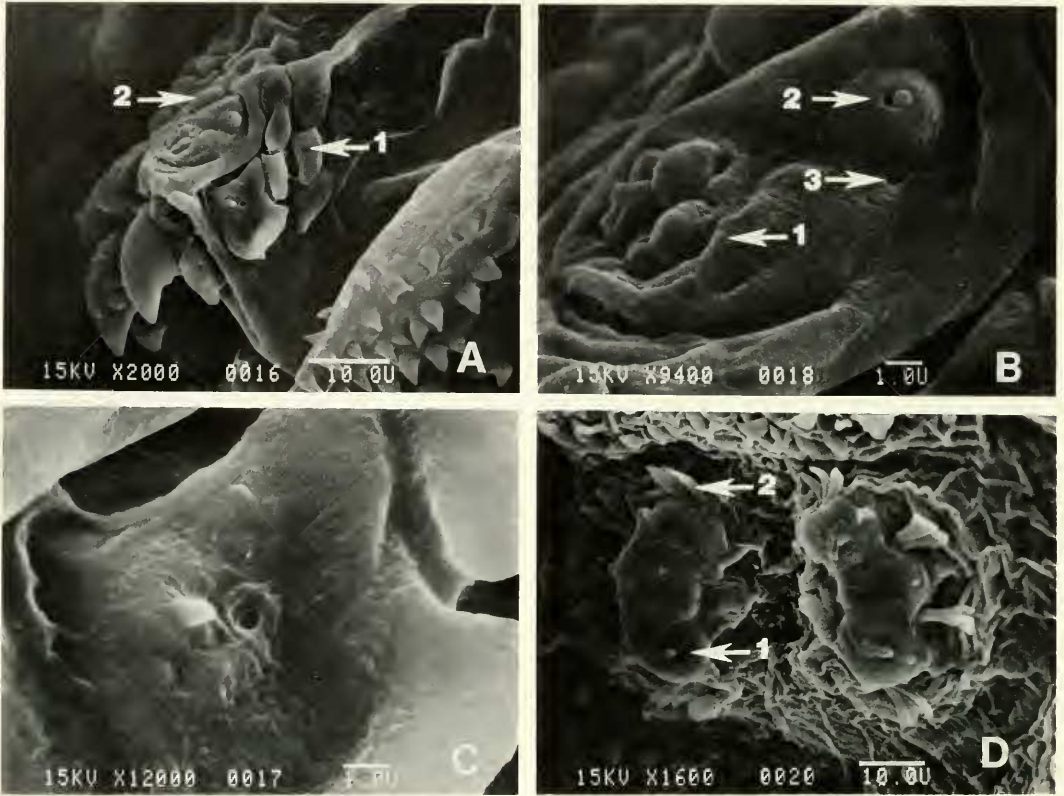


Fig. 3. Second-instar larva of *T. californica*. A. Anterior end, lateral view; 1, rugose pads; 2, dorsal sensory organs. B. Anterior sensory lobes; 1, terminal sensory organ; 2, lateral sensory organ; 3, pit sensory organ. C. Lateral sensory lobe. D. Posterior spiracles; 1, rimae; 2, interspiracular process.

long by 1.1 ± 0.02 (range, 0.8–1.6) mm wide. The anterior thoracic spiracles are located on the dorsal apex (Fig. 4B-1). The anterior end is distinctly invaginated (Fig. 4B-2) and lacks well-defined fracture lines which facilitate adult emergence. The posterior end is smooth (Fig. 4A, C). The largest spiracular rima (Fig. 4C-1) measured 0.04 mm in length and the longest interspiracular process measured 0.02 mm in length (Fig. 4C-2).

Distribution and hosts

Foote (1960) examined specimens of adults collected from 45 localities throughout California, including most of the those listed and mapped in Foote and Blanc

(1963). Foote and Blanc (1963) also included Arizona, Colorado, Nevada, New Mexico, Oregon, Texas, and Washington in the distribution of *T. californica*.

Rearing records of RDG from the following hosts and locations in California augment those reported by Foote (1960), Foote and Blanc (1963), and Goeden (1985): 11 males and 5 females, *Gnaphalium luteo-album* L., Cañada de Media, Central Valley, Santa Cruz Island, Santa Barbara Co., 7-x-1985; 25 males and 25 females, *G. microcephalum* Nuttall, S of Loleta, Humboldt Co., 2-ix-1985; 2 males and 4 females, *G. palustre* Nuttall, along Clear Lake Road at Fletcher Creek, 1600 m, Modoc Nat. Forest, Modoc Co., 25-viii-1989; 11 males and

6 females, *G. ramissimum* Nuttall, S of Loleta, Humboldt Co., 2-ix-1987. The preceding host records are new for *T. californica*. In addition, the following rearing records confirm published "unpublished" host records in Wasbauer (1972): 28 males and 37 females, *Anaphalis margaritacea* (L.) Bentham, ex C. B. Clarke, S of Loleta, Humboldt Co., 2-ix-1987; 2 females, *G. chilense* Sprengel, Figueroa Mountain, 1600 m, Los Padres Nat. Forest, 1-v-1985.

Goeden (1985) first reported *T. californica* from *G. beneolens*, *G. bicolor* Biolette, and *G. californicum* deCandolle. Since 1980, RDG (unpublished data) also has sampled but did not rear *T. californica* from four of the six other genera in the Tribe Inuleae that are native to California, i.e. *Antennaria* (n = 6), *Filago* (n = 3), *Micropus* (n = 1), *Pluchea* (n = 3). Thus, this tephritid apparently reproduces only in flower heads of *Anaphalis* and *Gnaphalium* spp. among California Inuleae. Other oligophagous, flower head-infesting species in California also show host preferences for different tribes, e.g. *Neotephritis finalis* (Loew) for the subtribe Verbesininae of the Tribe Heliantheae (Goeden et al. 1987) and *Tomoplagia cressoni* Aczél for the Tribe Mutiseae (Goeden and Headrick, unpublished data). Host preferences of most species of *Urophora* and *Neaspilota* for the Tribe Astereae in California were reported by Goeden 1987b, 1989). However, *Trupanea* spp. attack native hosts in nine of 12 tribes of California Asteraceae (nine of 10 native tribes) (Goeden 1985, unpublished data).

Unlike *Trupanea conjuncta* (Goeden 1987a), *T. californica* does not also facultatively form galls of terminal buds on the same species of host plant; however, at least one other species of *Trupanea*, i.e. *T. signata* Foote (Goeden, unpublished data) does form galls on *G. luteo-album*.

Foote (1960) noted the collection of adults of *T. californica* from species of *Artemisia*, *Parthenium*, *Prunus*, *Brassica*, and *Sola-*

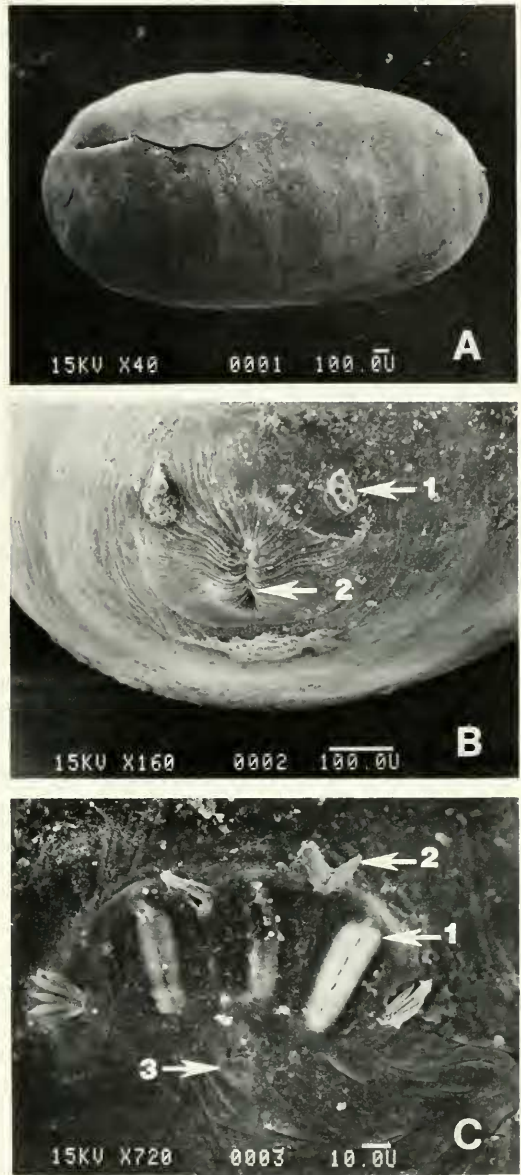


Fig. 4. Puparium of *T. californicum*. A. Habitus, anterior end at right. B. Anterior end, anterior view; 1, anterior thoracic spiracles; 2, invagination scar. C. Posterior end, spiracular plate; 1, rima; 2, interspiracular process; 3, ecdysial scar.

num, none of which are hosts of *T. californica*. This again demonstrated that sweep records for adults of flower head-feeding tephritids often are misleading as indicators

of reproductive host relations, as noted elsewhere (Goeden 1987b). More likely, swept adults were foraging opportunistically on nectar, pollen, plant sap at wounds and other sources of exudates, on homopteran honeydew, or were merely resting or seeking shelter on these non-host plants (Christenson and Foote 1960).

Biology

Egg.—Eggs were laid in immature, closed flower heads of *G. beneolens* in the field, usually in pairs, but also as one, or rarely, as three per head (Fig. 4a). The aculeus (ovipositor) is inserted in the notch between the tips of two outer phyllaries and pierces one or more underlying bracts in reaching the oviposition site. The eggs are laid side by side among, alongside, and with their long axes parallel to the floral tubes and pappus hairs. Their nonpedicellar ends rest just above the ovules. The eggs are lightly glued together along most or part of their lengths. The adhesive substance is transparent and thinly coats the egg body at oviposition, as reported for *T. imperfecta* (Goeden 1988), but does not engulf and obscure the non-pedicellar end, as described for *T. conjuncta* (Goeden 1987a).

No more than three eggs or larvae were found in each of 10 infested heads collected at Lake Hemet; however, in laboratory cagings, as many as six eggs were deposited in individual heads of excised inflorescences caged with a field-collected female for 3 days. This suggested that oviposition in individual heads in nature probably was limited by the short duration that the head is in a suitable stage, rather than by the deposition of a deterrent by a female after oviposition (flower head size probably also influences oviposition; see below).

Larva.—Newly hatched larvae tunneled into the ovules (Fig. 4b). Feeding is largely confined to the ovules and immature achenes, with no, minimal, or deep scoring

of the receptacle in *G. beneolens* (Fig. 1C). Only nine (4.5%) of 198 heads of *G. beneolens* contained three *T. californica* late-stage larvae or puparia (indicative of completed larval development), whereas 105 (53%) contained two individuals and 84 (42.4%) contained one individual. This host averaged 1.6 ± 0.41 *T. californica* per infested head. In heads with three individuals, little waste material was present in the open feeding chambers, the receptacles were deeply scored, and at best, only two flies had completed their development and emerged. In heads in which one or both larva(e) had died prematurely, the receptacle was less likely to be scored. Similarly, heads with only one larva or puparium usually contained a few intact achenes in a crescent along one side of the feeding chamber. Thus, the larva apparently scored the receptacle only after depleting most of the achenes, whereas in heads containing two or rarely three puparia (none of the latter heads yielded three adults), the receptacle was usually scored deeply. This suggested that the achenes provide insufficient food for three individuals to complete their development in heads of *G. beneolens*; i.e. one of the three larvae (eggs) was supernumerary.

Forty-five (90%) of 50 mature infested heads of *G. luteo-album* (generally smaller than *G. beneolens*, Munz 1974) yielded only one *T. californica* and five (10%) contained two individuals for an average of 1.1 ± 0.43 individuals per head. Among 50 mature infested heads of *G. californicum* (generally larger than *G. beneolens*, Munz 1974), 25 (50%) bore one individual, 19 (38%) bore two individuals, and six (12%) bore three individuals. This host averaged 1.6 ± 0.10 individuals per head, and some heads yielded three adults. Intact achenes remained in all heads of *G. luteo-album*, and the receptacles were scored in 48 (96%) of 50 heads. Intact achenes also remained in all heads of *G. californicum* attacked by *T. californica*, and the receptacles were scored in 44 (88%)

of these larger heads. Pair wise comparisons of mean tephritids per head at the 1% level indicated that *G. luteo-album* heads contained significantly fewer *T. californica* than the other two host species, which were not significantly different. This suggested that fly production was resource-limited only in the smaller size flower heads of *G. luteo-album*, to which *T. californica* apparently adjusted by laying fewer eggs. Interestingly, *T. californica* apparently did not take advantage of the greater resources offered by the larger flower heads of *G. californicum* by laying more than three eggs or producing more than three adults per head under field conditions.

Unlike several other nongallicolous, flower head-infesting species recently studied, e.g. *Paracantha gentilis* Hering (Headrick and Goeden 1990a,c), *Neaspilota viridescens* Quisenberry, and *Tomoplagia cressoni* (Goeden and Headrick, unpublished data), *T. californica* apparently has not evolved the behavior of switching as a third instar larva from ovule or achene feeding to scoring the receptacle to feed primarily on the sap that collects in the depression formed. Instead, *T. californica* continues to feed on the achenes, and may incidentally also score the receptacle during the last stadium.

Puparium.—When feeding is completed in heads of *G. beneolens*, one or two (rarely three) larva(e) pupariate within their separate feeding chambers in the achene layer. The long axes of any two puparia in the same head are either parallel or crossed, and their anterior ends are directed either upward and away from the receptacle or toward the same or opposite side(s) of the head. The smooth-walled feeding chamber is lined laterally with dried, reddish-brown, hardened plant sap- and liquid feces-impregnated debris and is defined above by a cap of apical fragments of achenes glued together laterally.

Many puparia in *G. beneolens* were oriented with their long axes perpendicular (or

nearly so) to the receptacle, as usually occurs with other flower head-infesting species of Tephritidae (e.g. Cavender and Goeden 1982, Goeden 1987a, 1988, Goeden et al. 1987, Headrick and Goeden 1990a, c). However, in smaller heads of *G. beneolens* and all heads of *G. luteo-album*, the orientation of the long axes of about half of the puparia was between 45° and parallel with the receptacle. Furthermore, in the 50 large heads of *G. californicum*, each of one to three puparia were oriented parallel to the receptacle within separate, peripheral feeding cells in which they rested alongside and lengthwise, touching the inner phyllaries (Fig. 1D). *Trupanea californica* thus provides the only example known to us of a nongallicolous, flower head-infesting tephritid that does not always, or nearly always, pupariate with its long axis perpendicular to the receptacle surface. Accordingly, when the adult emerges from its puparium, it crawls upward along the adaxial surface of the inner phyllaries to exit laterally from a flower head.

Adult.—Ten newly emerged females all contained immature ovaries, and like females of other stenophagous, synovigenic species of *Trupanea* studied to date (Cavender and Goeden 1982, Goeden 1987a, 1989), showed little abdominal fat-body tissue. *Trupanea conjuncta* and *T. imperfecta* usually remain sexually immature until their sole- or two-known hosts, respectively, resume flowering, which may not occur for a month or so after the flies emerge, or be deferred for as long as a year (Goeden 1987a, 1989). Like *T. bisetosa* (Cavender and Goeden 1982), however, *T. californica* has several host species on which it can mature and reproduce in sequence throughout much of the year in southern California.

Adults of *T. californica* are long-lived. Five males lived an average of 87 ± 16 (range, 59–149) days in the laboratory on a diet of honey and water; six females averaged 109 ± 17 (range, 52–156) days. No

sexual maturation or mating occurred with this diet.

Both males and females were quiescent at midday and active during mornings and afternoons. When at rest, both sexes groomed and pumped their mouth parts rapidly. Occasionally, a drop of clear liquid was issued and suspended from the pumping labella. The droplet was either imbibed and reissued or placed upon the substrate, where it dried to form a translucent spot. Another droplet might be produced within a few seconds after imbibition of the previous droplet (cf., Headrick and Goeden 1990b). One female produced three drops in a 15-min observation period and placed each droplet on the substrate after forming and imbibing them two to three times in succession. This behavior was observed in both males and females; moreover, both sexes produced similar size droplets of clear fluid from their terminalia. Females produced a droplet by extending the aculeus twice in succession almost to its full length while the droplet grew with each extension. The drop was formed subapically on the ventral surface of the extended aculeus, then placed down on the substrate. Males simply produced the drop from their terminalia and deposited it on the substrate. Such behavior may have helped to increase (by evaporation) the concentration of sugars and proteins in the watery food supplied under laboratory conditions.

Resting adults held their wings over their dorsa and parallel to the substrate such that the preapical stellate marks were contiguous but not overlapped (Fig. 1E). Spontaneous wing displays by both sexes occurred throughout the day. These displays consisted of alternate supination of each wing from a resting position over the dorsum and parallel to the substrate until the wing was nearly perpendicular to the midline of the body. During this wing motion, several discrete elements were observed. The wing was brought forward through an arc to where the costal margin was parallel with the sub-

strate. The wing blade was supinated through 90°, but the anal angle was projected forward even farther, and the wing was rapidly vibrated during the motion. Once the wing was supinated to its forward position, it was held there for variable durations, but usually for not more than 10 s. It was also noted that the abdomen was moved dorsoventrally three or four times in rapid succession after two or three wing displays. Males also tended more than females to display hamation of their wings when finishing with a wing display episode. Hamation is a new term defined here as the holding of the wings over the dorsum parallel to the substrate and moving them together from one side to the other through about 45°, usually done several times in quick succession. The wings are then held motionless in the typical resting position. Hamation is derived from the Greek pronoun *hama* meaning "together." Both sexes also rocked sideways back and forth during various phases of a wing display episode.

The wing display was often exaggerated if directed toward another adult. Each wing was brought forward through a higher arc, the supination was to a greater degree, and the wing was held out beyond the perpendicular plane so that the apex of the wing was as far forward as the head.

Males showed interest in females at about 1500 h PDT daily, by facing them stiling on their forelegs, distending their abdominal pleura (Fig. 1F), and displaying their wings. The wing display during courtship behavior was unique to the male and consisted of holding the wings upward at about 45° and away from the body at about 45°. The wings were rapidly vibrated in this position, but no supination or forward extension was involved. The abdomen was raised about 45° between the partially spread wings, and the antennae projected straight forward from the head.

Unfortunately, no female was receptive to a displaying male under laboratory conditions. A nonreceptive female either walked

or flew away, or boxed him with her front legs until he retreated. Sometimes, the male approached the female more passively; i.e. without abdominal pleural distention and with his wings held closely overlapped on his dorsum such that the preapical stellate marks on each wing were contiguous. Again, the nonreceptive female either decamped or showed aggression toward the male.

Aggression was frequently observed between caged couples. Each sex displayed aggression toward the other, which usually resulted in the nonaggressive individual walking or flying away.

Seasonal history

Trupanea californica is multivoltine in southern California. Adults have been reared from flower heads of different hosts collected during every month but December and January. No evidence of diapause was found in southern California. Like *Neotephritis finalis* (Goeden et al. 1987), *T. californica* reproduces on a succession of hosts throughout most of the year, exploiting flower heads produced at different times at different altitudes or for long periods by certain hosts in mild coastal areas and inland valleys.

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